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XIV.

ON THE COLOR AND THE PATTERN OF INSECTS.

BY DR. H. A. HAGEN.

Presented April 12, 1882.

"PROBABLY there is scarcely a dash of color on the wing or body of an insect of which the choice would be quite arbitrary, or which might not affect its duration for thousands of years." These words were written by Sir Charles Lyell in a letter to Sir John Herschel in 1836.* This letter, which is a real treasure of thought, asserts clearly that the writer assumes "such contrivances must sometimes be made, and such relations *predetermined* between species," for the protection of their existence.

Though it has been accepted generally that certain colors and patterns of insects might be a protection against enemies, these interesting facts have been mentioned only occasionally, and a general review is still a desideratum. Professor Weismann † has given a very elaborate paper on the origin of the pattern of caterpillars. The paper, as stated in the preface, intends an examination of the pattern strictly for the purpose of finding out whether all patterns can be accepted as the consequences of selection and adaptation, and as produced in a *purely mechanical manner*, or whether some unknown power has to be accepted in part or entirely to explain the pattern. The writer reaches the conclusion that the latter is not the case, and that the known principles of selection and adaptation explain the different patterns. The choice of caterpillars was made purposely to exclude entirely a third factor, sexual selection. Everybody will follow Professor Weismann's careful and elaborate study with interest, though it is probable that the examination of a larger number of exotic species (he hàs chiefly used European) will change, or at least modify, some of his statements.*

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* Life, Letters, and Journals of Sir Charles Lyell, Bart., London, 1881, vol. i. p. 469; Nature, No. 633, Dec. 15, 1871, p. 147.

† Dr. A. Weismann, Studien zur Descendenz-Theorie, Leipzig, 1875, vol. i.; 1876, vol. ii. Die Entstehung der Zeichnung bei den Schmetterlings Raupen.

Nevertheless, if it is to be assumed with Professor Weismann that the colors and the pattern originate in a purely mechanical manner, there seems to be a large gap still to be filled. The statement that color and pattern appear in a caterpillar by selection and adaptation as a beneficial protection, without showing how they have been produced, where they come from, which part of the body, and what kind of chemical process brings them out, represents simply a belief. Belief is, as it is well known, beyond discussion, as long as it is based upon views which cannot otherwise be proved. But as the author has prominently advanced that the origin of the color and the pattern is only the consequence of mechanical arrangements, excluding entirely predetermining power, the possibility of such mechanical arrangements should have been proved satisfactorily.

If we compare side by side Sir Charles Lyell's letter with the accepted predetermination and Professor Weismann's work with the denied predetermination, there seems to be no difference except in the belief of both authors.

The conviction that color and pattern are the consequence of existing laws and actions in the body of the insect, induced the present writer to extend his study in that direction. May it not be considered too assuming, if the result shall prove inadequate to the purpose. The first step in all such questions is the most difficult, and often nothing more is left to be said about it, except that it was the attempt of the first step.†

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* Of North American Sphingidæ the previous stages of fifty-four species are known, and of fifteen species all stages. With very few exceptions all were published before 1874. Of the European species all stages were described long ago of eight species: *Sphinx ligustri* by Schwarz; *Sph. pinastri* by Sepp, Ratzeburg, Hartig, Schwarz, Klopsch; *Deil. euphorbiæ* by Sepp, Rösel, Schwarz; *Deil. porcellus* by Sepp; *Smer. tiliæ* by Rösel, Reaumur; *Smer. ocellata* by Sepp; *Smer. populi* by Sepp, Schwarz; *Deil. nerii* by Rossi. With few exceptions excellent figures are given. The literature is therefore not so scanty as has been assumed, though not sufficient for the purposes of the author.

† Some parts of the present paper were published in the Amer. Natural. 1872, pp. 388–393, and Entom. Monthly Mag. 1872, ix. pp. 78–83, Mimicry in the Colors of Insects.

The Color.

As most insects are more or less colored, color is an important character. I have said purposely insects, and not arthropods, because my studies have not extended to the other groups. Some facts, of course, can be applied to all; but the other groups are not to be compared for the frequency and for the intensity of the colors with those of insects. There is no doubt that the different colors of insects are the consequence of the contact of the animal with air and light; or at least that colors are more strongly developed by both these factors. The only contrary statement known to me is by Professor Sachs, and will be considered later. The influence of light is proved by the colorlessness of cave insects, of the larvæ living in the earth or in the interior of plants or animals, even by some insects living only a very short time in the open air, as certain very small Ephemerina and Diptera. It is proved by these facts that colors of organic bodies, plants, and animals are found prominently in their external coverings. Therefore the Greek philosophers considered color to be the product of a chemical action, called by them πέψις, boiling. The interior of organic bodies is mostly colorless or discolored. There exist, indeed, exceptions even in insects, but at least a part of these internal colors is to be found in places which are in contact with the air. The tracheæ in Odonata and others are red; the fat body in Trichois red, in Zerene yellow, in Pentatoma green; the Malpighian vessels in some Orthoptera green; the testicles in some Hemerobina, at least in the previous stages, lemon yellow; the anal glands in Osmylus black; the blood in Chironomus red. In other orders we find some internal organs of Holothuria brick-red, of Echinus yellow. After all, we are justified in considering those cases as exceptions, or even as rare ones.

Besides air and light, there is a third factor influencing the development of color, heat and its counterpart, cold. The heat has a well-known prominence in all chemical processes, and of course also in colors if they are the result of a chemical process. The carbonizing of tissues gives to them a certain color by the change which follows the combination of the tissue with oxygen. Such colors are very common, and of different intensity in insects. The brown or black color of many chrysalids, which are inclosed in a cocoon not permeable to the rays of light, is probably the product of carbonization. The importance of heat and of cold for the production of colors in insects has lately been shown by careful and convincing experiments by Dorfmeister,* Weismann,† W. H. Edwards,‡ and others.

The remarkable influence of a wet or dry atmosphere on the colors will be considered later. The interesting albinism and its counterpart, melanism, have not yet been studied to such an extent as to allow of decided conclusions. Albinism is much rarer among insects than among birds; but it is obvious that a satisfactory explanation of these aberrations would permit conclusions about the nature and origin of the colors.

Besides chemical colors, there exist a very different kind, optical colors, which we will consider first.

Optical Colors.

Optical colors, produced by the interference of light, are by no means rare among insects, but they are solely optical phenomena. Colors by the interference of light are produced in two different ways: either by thin superposed lamellæ, or by many very fine lines or small impressions in very near juxtaposition.

There must be present at least two superposed lamellæ to bring forth colors by interference. There cannot be more than four layers in the wings and scales, which show principally such colors in insects, two external ones belonging to the cuticula, and two internal ones belonging to the hypodermis. The naked wings of Diptera and Neuroptera often show beautiful interference colors.

The scales of Entimus and other Curculionidæ are well known for their brilliancy, and it is interesting to remark that when dry scales are examined with the microscope, many are found partly injured, which give in different places different colors, according to the number of layers which remained. The elytra of some Chrysomelina and other beetles with iridescent colors orobably belong to the same category.

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* G. Dorfmeister, Mittheil. des naturwiss. Ver. f. Steiermark, 1879, pp. 3-8; Ueber den Einfluss der Temperatur bei der Erzeugung der Schmetterlings Varietäten (*Vanessa Atalanta*), and ibid. 1864 (not seen by me); Ueber die Einwirkung verschiedener während der Entwicklungsperiode angewendeter Wärmegrade auf die Färbung und Zeichnung der Schmetterlinge.

† Ueber Saison-Dimorphismus der Schmetterlinge, 1875, vol. i.

‡ Mr. D. W. Edwards' (Coalburgh, West Virginia) papers are published, Canad. Entomol. 1875, vol. vii. p. 228; 1877, vol. ix. pp. 18, 203; vol. xiv. 1882, p. 21; Psyche, 1880, vol. iii. Nos. 69, 70; 1881, vol. iii. No. 83.

Since science is so far advanced, that for every color produced by interference of light the distance of the lamellæ is known by calculation, it would be possible to give the exact figures of the distance for every color observed on insects. The wings of some insects show interference colors only for a certain time (Chrysopa, Agrion), as long as the membranes of the wings are soft and not firmly glued together. Later those wings become simply hyaline. On other insect wings those colors remain during lifetime and persist even after death.

Secondly, interference colors are produced by many very fine lines or striæ in very near juxtaposition. Such colors are easily observed by looking in an oblique direction towards a glass micrometer, even not a very finely divided one. Some forty years ago Mr. Barton, a manufacturer in London, used to make iridescent buttons called iris buttons. There were only thirty to forty impressed striæ on a square line. But each adjacent square line had the striæ in another direction. The fine longitudinal and transversal lines of the Lepidopterous scales seem to serve admirably well to produce the brilliant effect of color-changing butterflies. But there must be something more present, as most of the scales of Lepidoptera are provided with similarly fine lines, and only comparatively few species change colors. I remark purposely that the lines in the color-changing scales are not in nearer juxtaposition. The explanation of the fact given a century ago by Rösel,* stating that both sides of the lines (like small prisms) were differently colored, was due to an optical illusion, explained by the insufficient power of the non-achromatic microscopes at that time. There may be a way of explaining this kind of iridescence not yet used by naturalists; I mean calculation. The late Mr. Nobert, of Greifswald, the unrivalled maker of the well-known test-plates, which contain bands differing by the number of lines, had so far advanced that the last band has lines with less than one 100,000th of an inch distance, where the delicate lines of Diatoms are separated from each other by one 50,000th of an inch. Some twenty years ago there did not exist microscopes strong enough to see those lines, and it was doubted by the French Academy if they were really present. Mr. Nobert, as accomplished in mathematics as in mechanics, proved by calculation based upon the interference colors produced by those lines, the space between them. The result agreed perfectly with his previous assertions. Now the most powerful microscopes show the lines, and they have been photographed of every band by Dr. Woodward in Washington. But even now science is not entirely equal to mechanics, as the photographs show by some optical illusion six or more lines than were made by Mr. Nobert. Perhaps in the color-changing butterflies natural colors are combined with optical colors, or perhaps interference colors produced by superposed lamellæ are combined with those produced by fine striæ. It will be necessary to deprive the wings of their natural colors by bleaching, and then to make a microscopical examination. I have begun experiments for this purpose. The wings of *Apatura clytie*, a variety of *A. ilia*, are pale yellow in the color-changing part; the wings of *Euploea superba* are velvety black above, the black changing into violet in the color-changing part. Both wings, put in eau de Javelle, began to grow pale after one hour. The paleness began first in the color-changing part of *E. superba*, and was less visible in the much lighter-colored wings of *A. clytie*. After one hour and a half the whole color-changing part of both species was entirely hyaline. The not color-changing parts were very little affected, and in *A. clytie* the light-brown spots were nearly intact. Both wings had lost entirely the change of colors. The microscopical examination showed that the scales of the color-changing parts were very much affected. The scales were hyaline, nearly invisible; the longitudinal striæ less sharp, the transversal ones even more affected, and mostly obliterated. In some places in the middle of the color-changing part the scales had disappeared, and only their stems were left. On the other hand the scales of the not color-changing parts were nearly unchanged, and both kinds of the striæ as sharp as before. The under side of the wings does not change color at all, nevertheless the parts corresponding to those iridescent ones of the upper side were affected as much and in the same manner as the scales of the upper side. From the beginning of the bleaching process both sides made the same progress in becoming hyaline. Now the striæ of the scales, though they had been much affected by the bleaching, could not be the producers, at least not alone, of iridescence, as in all not color-changing scales the striæ are exactly of the same arrangement and distance, just as fine and approximate as in the iridescent ones. Therefore it may be presumed that the lamellæ of the iridescent scales are more distant one from the other, less firmly glued together, and therefore easier affected by the bleaching fluid and the colored substance between the lamellæ easier bleached. But why are the corresponding not iridescent scales of the under side of the wing also affected, and at the same time with those of the upper side? It can only be supposed that the quick effect upon the scales on one side of the wing gives easier access to the scales on the other side. I confess that I am not entirely satisfied with this explanation, but I do not know of a more satisfactory one. For the first experiment the wings were cut through the middle of the color-changing part, and were therefore perhaps more quickly affected. In subsequent experiments with entire wings of *Euploea superba* the iridescence was gone in three-quarters of an hour, but the wing was only less dark even in the color-changing part. In the same space of time wings of *Apatura Iris* and *Ilia*, and of *Thecla quercus* were entirely bleached, those of *Lycæna Damon* only partly. The question whether the striæ of scales with more distant lamellæ will help to produce iridescence, which the same kind of striæ of scales with not distant lamellæ does not do, I am unable to answer.

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* A. J. Rösel, Monatliche Insecten Belustigung, 1755, vol. iii. p. 256, pl. 44.

The colors of butterflies change mostly from purple to blue, sometimes to yellow. Probably a calculation based upon the appearance of these colors might help to solve the question.

An interesting observation by Professor Graber* is here to be noticed. When caterpillars of Apatura are kept in diffused light, the wings of the butterfly show almost no iridescence. The wings of *Vanessa polychloros* have slate-colored marginal spots instead of the commonly blue ones, when the caterpillars are raised under yellow glass. As no authority is quoted, these observations may have been made by Professor Graber himself. It is obvious that here a new and interesting field for experiments is open. The record of Professor Graber's observations is too fragmentary to go farther with conclusions based upon them, the more so as such isolated experiments need always the support of reiterated observations before they can be accepted as facts. This would be needed here even more, as it is difficult to understand how a different light could work through the skin of a caterpillar on the wing of the imago which is scarcely beginning to be built up in the interior of the caterpillar. If true, it would be an important discovery. An observation by G. Schoch† does not corroborate Professor Graber's statement, at least for the changing of colors. *Euprepia caja* was raised by him in different colored light. The caterpillars were kept in three boxes, covered with red, violet, and blue glass. Those under violet glass were more voracious than the others, and consumed twice as much food. Their crysalis transformed in the imago a fortnight earlier than the others. But the imagos of all did not show any perceptible difference. Perhaps raising of the caterpillars in diffused or homogeneous light may have a different effect, at least for iridescent butterflies. The Newton color rings viewed with homogeneous (yellow) light change the color of the rings, the dimensions of which grow smaller and smaller between the red and violet rings, in a proportion from fourteen to nine. I do not know that iridescent butterflies have been examined under homogeneous light; perhaps such experiments would allow further conclusions.

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* V. Graber, Insecten, 1877, vol. ii. p. 38.

† G. Schoch: Mittheil. d. Schweizer entom. Gesell. 1880, vol. v. p. 540. Zucht von *Euprepia caja* im gefärbtem Licht.

Krukenberg * presumes the golden-green color of *Carabus auratus* to be an interference color. It is not changed by the influence of light, nor was he able to extract from the elytra any green pigment with ether, benzol, carbon of sulphur, chloroform, alcohol, even after having submitted the elytra before to the influence of muriatic acid or ammonia. Chlorophyll is not present, whether free or combined with an acid. The chlorophyll found by K. B. Hofmann (Lehrbuch der Zoochemie, 1875, No. 3, p. 368) in the elytra of Cantharis is not present in them, but is derived from the contents of the alimentary canal. The change of the color in Cantharis is probably the consequence of an alteration of the chitinous external integuments by cold weather or by a more elevated habitation.

Interference colors are also produced by very small impressions in juxtaposition. Such an arrangement is found on the feathers of birds; for instance, on the necks of pigeons and elsewhere. In the hairs of Aphrodite and Eunice this arrangement may be compared with striæ (Leydig). Perhaps this kind of interference colors is found more frequently among insects than is commonly known. At least there are often parts of insects, and their limbs in appearance yellowish, but in a certain direction changing to brown or blackish. I know of no other explanation of this not uncommon fact on the legs of Diptera, of Hymenoptera, and of Phryganidæ. G. Pouchet (Des Changements de Coloration sous l'Influence des Nerfs, Journ. de l'Anat. et Physiol.,

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* C. Fr. W. Krukenberg: Vergl. physiolog. Studien an den Küsten d. Adria, 1880, 1881, vol. iii. p. 62.

Paris, 1876) has drawn attention to the so-called Iridocystes (Interferenzellen of Brücke). They do not belong to the pigment, but to optical colors, to fluorescence. A large number of small superposed lamellæ become luminous by contraction. They are very brilliant in Saphirina and in a large number of fishes, allowing them to change color according to the color of the bottom on which the fishes are standing. They may occur in some insect larvæ, but have not yet been recorded. I believe that the arrangement in some insects' eyes (Mantis), to be mentioned later, belongs to the Iridocystes. It should be remembered that interference colors, one or both kinds, may occur in the same place together with natural colors. The mirror spots of *Saturnia Pernyi* show besides the interference colors a white substance in the cells of the matrix, which Leydig believes to be Guanin. But this fact is denied by Krukenberg for the same species, and also for *Attacus mylitta* and *Plusia chrysitis* (vol. v. 1881, p. 65).

Natural Colors.

There exist two different kinds of natural colors.

1. The pigment is deposited in the form of very small nuclei in the cells, or in the product of cells, in the cuticula.

2. The pigment is a homogeneous fatty substance, a kind of dye somewhat condensed.

Pouchet speaks of a third kind of natural colors, which are said to be inherent to certain tissues. He mentions them only for the muscles, as I believe erroneously. So I have dropped entirely this kind of colors till a more sufficient proof for their existence is given.

The first kind of natural colors is to be compared with pigment inclosed in air-tight glass tubes; the second is related to a diffusive or fluid pigment.

The first kind of colors belongs to the cuticula, and I will call them *dermal* colors. I consider them to be produced mostly by oxidation or carbonization, in consequence of a chemical process originating and accompanying the development and the transformation of insects. To a certain extent the dermal colors may have been derived from hypodermal colors, as the cuticula is secreted by the hypodermis, and the colors may have been changed by oxidation and air-tight seclusion. The cuticula is in certain cases entirely colorless, — so in the green caterpillar of *Sphinx ocellata;* but the intensely red and black spots of the caterpillar of *Papilio machaon* belong to the cuticula, and only the main yellow color of the body to the hypodermis (Leydig, Histiol., p. 114). A particular main color of the cuticula is assumed by Graber (p. 17), which is said to change the underlying hypodermal colors. As far as my studies go, the color of the cuticula is often somewhat yellowish with a brownish shade, and only the most superficial layers contain pigments, which therefore must have been produced during or directly after the casting of the skin. The layers below the superficial ones were of indifferent color and had nothing to do with the main color of the insect (thorax of *Phanæus carnifex*). Whether this is generally true will be proved by farther observations.

The second kind of colors belongs to the hypodermis, and are called *hypodermal* colors. I consider them to be the consequence of a chemical process, generating color out of substances contained in the body of the insect. These colors may be changed into other colors by light and heat, perhaps by acids or by the influences of the sexual organs. If such a change were to a certain extent a photographic process, some important facts (mimicry) could be understood, which otherwise are inexplicable.

The dermal colors are red, brown, black, and all intermediate shades, and all metallic colors, blue, green, bronze, copper, silver, and gold. The dermal colors are easily to be recognized as such, because they are persistent, never becoming obliterated or changed after death. Dermal colors are not unfrequently retained by insects inclosed in copal, but never by fossil insects inclosed in amber. The persistence of dermal colors is easily understood, as they are formed before the chitine becomes rigid, and later are preserved in a similar manner as if they were inclosed in hermetically-sealed glass tubes.

The hypodermal colors, placed in the soft and not chitinized hypodermis, are easily recognized, because they fade, change, and disappear after death. A fresh or living insect, when opened, can easily be deprived of the hypodermal colors, simply by the action of a small brush. An important exception is to be made in certain cases, in which hypodermal colors are persistent after death as well as dermal colors. In such cases the colors are better protected and inclosed nearly air-tight. I refer to certain colors of the elytra and wings, of the hairs, scales, and appendages of the body. The elytra and wings are, as is well known, at first open bags in direct communication with the interior of the body. The hairs and scales are at first similar open bags, glued together only at a later period. In all of them the hypodermal colors are formed, of course, before the membranes are glued together; after that time those hypodermal colors are nearly as well preserved as dermal colors, except that they are subject to fading after a lapse of time. The possibility of such an inclusion is proved as a fact by the inclusion of air in the white scales of Lepidoptera. The white mother-of-pearl spots of the species of Argynnis are produced by a system of fine transversal pore-canals filled with air; by Hydrometra the white ventral marks have the same origin (Leydig).

The hypodermal colors are mostly brighter and lighter than the dermal ones, — light blue or green in different shades, yellow to orange, and the numerous shades of those colors combined with white. Exceptionally they are metallic, as in Cassida, and are then obliterated after death. The fact which I find quoted, that such metallic colors can be retained in dead specimens by putting a drop of glycerine under the elytra, allows us to conclude that those colors are based upon fat substances. The hypodermal colors are never glossy, as far as I know; the dermal colors frequently.

It must not be overlooked that elytra, wings, and hairs all possess a cuticula, and that even here dermal colors are frequently to be found, together with hypodermal ones, chiefly in metallic colors. In the same place both colors may be present, or one of them alone. So we find hypodermal colors in the elytra of Lampyridæ. In the elytra of the Cicindelidæ the main metallic color is dermal, the white lines or spots are hypodermal; by which arrangement the variability in size and shape of those spots is explained. A large number of Lepidoptera have hypodermal colors in the scales of the wings, — a fact shown by the rapid fading of those species.

There occur in a number of insects external colors, that is, colors upon the cuticula, which I consider to be in fact displaced hypodermal colors, — the mealy pale blue or white upon the abdomen of some Odonata, the white on many Hemiptera, the pale gray on the elytra and on the thorax of the Goliath beetle, and the yellowish powder on Lixus. Some of those colors dissolve easily by ether or melt in heat, and some of them are a kind of wax. I believe that those colors are produced in the hypodermis, and are exuded through the pore canals. Therefore they may be considered as belonging to the hypodermal colors. *Eriosoma alni* is commonly covered with white waxy secretions. When taken off gently a new secretion soon begins to appear out of the pores of the four circular glands which are found on each segment of the abdomen. If the dorsal half of the abdomen of a female is cut off, the fluid contained in the body by its contact with the air changes directly to a white shade, which seems to be of the same nature as the external secretion. Therefore this white secretion would not be strictly derived from the hypodermis, except that it is secreted by hypodermal glands. I am not sure whether some of the colors before mentioned may not be in some way different from the others. In the case of Lixus I find it stated that the mealy powder, when taken off, is renewed in a few days. I confess that my opinion concerning those external colors is not yet entirely settled. That those colors are simply an exudation of fluid in the body through the pore canals is not to be accepted; they must have been changed in passing through the hypodermis. In such Lepidoptera as become oily after death, the fat exudes through the pore canals, and, passing through the hypodermis, reaches the outside of the body unchanged. A chemical investigation would be very desirable, and would perhaps give some better explanation; but the quantity which may be had of those colors is always too small for such a purpose. The blue mealy matter of the abdomen of Odonata when scratched off and brought in contact with ether on a glass slide is directly dissolved, leaving scarcely a margin around the spot after the evaporation of the ether. When the same matter on a glass slide is held over a candle, it melts directly, and after drying a dull whitish spot is left.

Bezold's Views upon the Nature of Colors.

Recent investigations about the nature of colors advance also our knowledge of the colors of insects. The Theory of Color in its Relation to Art Industry, by W. von Bezold,* contains some excellent statements, which allow us to understand better the colors of insects.

1. " *Transparent colors*, so called by artists, are similar in their action to colored glass or to clear-colored solutions. When the light falls upon a shining surface of such colors, a reflection primarily takes place at the upper surface, extending only to a fraction of the impinging light; the remainder enters the colored mass, and there undergoes a process of absorption, so that it is already decidedly colored when it arrives at the ground-surface of the layer. If at this second surface the light strikes upon a white body which reflects irregularly,

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* Dr. W. von Bezold: The Theory of Color in its Relation to Art and Industry. Translated by S. R. Köhler, Boston, 1876, &c.

colored rays will be emitted from this layer in all directions which face toward the impinging ray of light, and in the repeated penetration of the colored layer their color will increase in intensity."

I am not yet prepared to assert with certainty that such transparent colors exist in insects. It is obvious that the different layers of the cuticula, when possessing a peculiar color, would answer exactly the conditions above stated, the more so as a glossy surface is frequent among insects. Perhaps some remarks by Graber (Insecten, i. p. 17) belong here. "Most frequently the hypodermis is colored brown or red, even in such insects as are externally entirely green, as the grasshopper, or black, as the cricket. This fact is to be explained partly by the refraction of the cuticula, and partly by its peculiar color." If Graber's observation proves to be true, the explanation will be sufficient, and then we have a right to assume that similar cases may occur among insects. Transparent colors would belong to the dermal colors, modified perhaps by the underlying hypodermal colors.

2. "*Body colors* in an artistic sense [Bezold, p. 57] differ entirely in their action from transparent colors. They are likewise transparent in very thin layers, and with them it is also the light that has passed through the pigment which exhibits the characteristic color of the latter; but the great difference in the optical action of the pigment and of the medium, makes it impossible for the light to penetrate through layers of any perceptible thickness. On account of this difference a division in transmitted and reflected light takes place at all the surfaces of separation of the particles of the coloring matter, so that the portion of transmitted light is already reduced to an almost inappreciable quantity at an insignificant depth below the surface. The same is of course true of the light sent forth by the lower surface, and this explains why such colors are opaque when applied in tolerably thick layers. The light reflected by body colors will always contain a larger quantity of white light than light that is reflected by transparent colors. This is the reason why that brilliancy and depth or fulness can never be attained by body colors as by transparent ones."

It is therefore obvious that just this kind of color is very frequent among insects, and not only in dermal, but also in hypodermal colors, when the cuticula covering them is perfectly hyaline.

3. "*Surface colors* [Bezold, p. 61] are the consequence of bodies which cause a division of the light falling upon them, which allow rays of a specific degree of refrangibility, or, in other words, of certain

colors to enter, while they reflect all others. Such bodies show one color when the light falls upon them, and another when the light is transmitted through them. The metals in very thin leaves are especially prominent in this class of bodies. The various aniline pigments also show such surface colors when dry. Thin layers of those pigments will have a perfectly metallic appearance. Fuchsine or Magenta has a green golden color when the light falls upon it, a purple color when the light is transmitted through it."

The surface colors are prominently interesting for entomology, as they explain for the first time the frequent metallic colors on insects, which have often so true a metallic appearance, that indeed it has been tried to extract the gold out of them. The condition that such layers must be perfectly dry, makes it evident, as I have before stated, that metallic colors must belong to the dermal ones. As I have stated later, that insect colors might with propriety be compared with aniline colors, the whole comparison is even more to the point.

4. "*Fluorescent colors* [Bezold, p. 621] act quite differently from the before-mentioned ones. In all those cases a division of the impinging rays took place, so that a part of the rays entered the body or passed through it, and that the remainder was absorbed or reflected. But the fluorescent bodies transform the light falling upon them into light of another color, that is to say of different wave-length. This is frequently observed in the yellowish-green uranium glass, in fluorspar, in solution of quinine, in petroleum and other bodies. Investigations with the aid of the spectrum show that in the case of bodies of this kind light of the most varied colors is transformed into light of some other definite color, and that even invisible rays can be changed into visible ones, as the ultra-violet rays. The retina possesses in a slight degree the property of fluorescence." I presume that a number of insect colors may probably belong to this kind, namely, the violet shades observed in Rutela and similar beetles.

I have purposely dwelt at length on these phenomena, as I believe that they will throw considerable light upon occurrences till now unexplained.

Hypodermal and Dermal Colors.

The hypodermal colors are very often different in males and females of the same species. The dermal colors rarely differ, so far as I know, in the sexes. But there are some genera with prominent dermal colors, which are nearly always different in both sexes, as Calopteryx, some Hymenoptera, some Coleoptera, and others.

It would be interesting to know exactly the rule for the change of color in males and females. So far as I know, this change seems to be between related colors, and not between complementary ones. But my observations are far from having any conclusive importance; in some cases, as in Hetærina, the change is effected by complementary colors, red and green. The same investigation will have to be made for hypodermal colors. As far as I know, even here the change seems commonly and chiefly between related colors; though some cases of complementary colors have been observed.

The dermal colors never change during lifetime; the hypodermal ones may be changed in some way, and are known to be altered in some instances in a male or female during its lifetime, by sexual or other influences. By sexual influences, for instance, yellow is changed into orange, brown into red (in some Agrion females), milk-white into blue in males, and into green in females (Platycnemis). By other influences, for instance, by cold (Brauer) in hibernation, pale yellow is changed partially into red (Chrysopa). But this change is said to be produced by chromatophores by other naturalists (Leydig). The hypodermal colors in one insect (*Cassida aurichalcea*) are stated to be changed by a voluntary act of the insect, and the new color can again disappear (Harris).

Sexual Selection.

Everybody has studied with interest in Mr. Darwin's works (Descent of Man, vol. i. p. 374; Nature, vol. xxi. p. 237, No. 532) the exposition of his theory of sexual selection. The part concerning the butterflies is a rather prominent one. But when we weigh the given facts, they do not seem to be so conclusive as they are considered to be. Comparatively *very few species* agree very well, or only well, with Mr. Darwin's assertions. The fact that it is only peculiar to butterflies, and does not occur in other families of Lepidoptera, becomes more important when we find that the theory is exemplified only in less than one per cent of the butterflies themselves. Why is the whole main army so much behind? — is a question nowhere found answered. After all, the statement, that the male is so much more beautifully colored for sexual selection, will apply only to exceptional cases among Lepidoptera.

Papilio turnus in North America offers a rather puzzling case. Its southern dark-colored female, formerly *Papilio glaucus*, will be as good an example as any other for an indifferently colored female of a beautifully colored male.

But unfortunately it happens that all the females of *Papilio turnus* in the northern half of North America are so presumptuous as to show the same gay colors as the male, and even brighter and more variegated ones. Both sexes have as caterpillars the same food in the South and in the North. The chrysalis of the dark and gay-colored females is not different, except that I find in two of the dark ones raised by J. Boll in Texas (there occur both forms) a longitudinal blackish ventral band which is not to be seen in the chrysalis of the gay-colored females. There is, therefore, no reason left to understand why this species should form such a strong exception. If the males need something besides beauty in their competition for the females, it seems as if the strongest would always be the winner. But is it sure that the most prominent external beauty always coincides with the most prominent sexual power? I confess that I have some doubt about the fact, as the artificial loss of this power by castration is followed in birds, in mammals, and in an isolated instance in fishes, by an unusual development of external beauty.

The Change of Color.

The color of insects, or at least its changes, may be originated by the influence of the air and its humidity, of the temperature, of the season in which they appear, of the character of the country.

The facts to elucidate such important and interesting changes are still scarce and isolated. The curious season dimorphism belongs here. The facts stated in the publications of Weismann and W. H. Edwards are known to every student, and need not be repeated here.

The darkening influence of a climate or country with a large amount of average humidity, which is so well proved for vertebrates by Mr. J. A. Allen, has a similar effect on insects. The peculiar coloration of animals living in deserts is well known, and to a certain degree repeated among insects. The brilliancy of colors in the tropics has become long ago a commonplace remark. Surely there are to be found in the tropics the most brilliantly and intensely colored animals, but it must not be forgotten that by far the largest number of insects in the tropics are just as indifferently and as darkly colored as those in colder regions.

It is a remarkable fact that cold or arctic regions, where snow and ice prevail, do not form, concerning the color of insects, a counterpart to the tropics to the extent we might expect. Of course we find there white or pale-colored species, but they are by no means numerous, and the so-called winter insects, which are found on the snow, are mostly dark brown or black. But even in the coldest regions beautiful and gayly colored species occur, but mostly yellow, orange, or red ones.

An interesting and only recently studied fact, is the change of colors of the same insect in different countries. Some valuable hints are given by Dr. Speyer (Stettin. entom. Zeit. 1875, p. 103). If the predominant colors of Noctuidæ are gray, brown, or reddish brown, or rather a mixture of black, white, and red, less red and more black has been observed in North American specimens, and less black and more red in European ones of the same species. If the colors are a mixture of yellow and red, just the opposite change is seen; in the North American specimens the red is predominant, in the European ones the yellow.

A few words more about beautifully colored caterpillars. As sexual selection could not have acted here, and as it was observed that some of them were not taken by certain species of birds and lizards, but purposely avoided by them, it was supposed that the splendid color serves here as protection. But if we remember that some birds prefer certain caterpillars, and other birds others, as, for instance, the hairy caterpillars, whose hairy cover suggests the idea of protection, we shall arrive at the conclusion that more observations are needed to confirm the above-quoted supposition.

Water insects are nearly all of the same dark hue, yellowish brown to black, often with an olive shade. Only parts of the body which are uncovered in the air (abdomen of Nepa) are sometimes of a brighter purple color. But even among water insects some are to be found (Hydrachna) of an intense red color.

The climax of the development of the pure and elementary colors seems to be reached in the class of insects. All these colors appear here without any transition whatsoever, even in close juxtaposition.

The Pattern.

The pattern of the colors of insects is a subject very important for every naturalist who studies or describes insects. Till to-day only very little has been published about the pattern. Something is stated by monographers about certain groups or families, but that is all. I believe that a more detailed study of pattern and of the different patterns which are to be found in different groups, and perhaps the development of the law according to which the pattern is changed in different groups, would advance us nearer to the knowledge of its nature and origin. What I know about it is only the first step in this direction.

The pattern is not the product of an *accidental circumstance*, but apparently the consequence of certain events or actions in the interior of the insect, mostly at the time of its development. The proof is easily afforded by the regularity of the pattern in the same genus or in the same family. If studied carefully and comparatively, the pattern of such a genus is the same for all species, but for some of them more or less elaborated. The number of such genera, and even of such families having the same pattern, is so large, that some will be readily remembered by every naturalist. In some families a peculiar and constant pattern can be observed for the head, a different one for the thorax and its limbs, and again another one for the segments of the abdomen. The latter is on the different segments (Hymenoptera, Diptera, Neuroptera, Pseudoneuroptera) mostly the same, but more or less elaborated, and less finished in the first and last segments. To a certain extent the same can be said about the segments of the thorax.

Weismann has studied carefully the origin of the pattern of caterpillars of the Sphingidæ. The caterpillars were chosen by him because sexual selection is thus excluded. When just hatched they are mostly colorless, but after a few hours they almost always become uniformly green.* The pattern appears generally after the first moult in the form of longitudinal bands or lines. There is a dorsal line, and one on each side a subdorsal one, and lower down one along the stigmata. In Chærocampa the subdorsal line is changed on two segments of the thorax into large eye-spots, and disappears entirely on all the following segments. In Deilephila the same line forms a ring-spot on the last segment, which in some species is repeated in former segments. In Smerinthus oblique lines cross the subdorsal line on each segment, and these oblique lines receive colored borders in Sphinx and Acherontia. The caterpillars of Chærocampa and Deilephila change later the green color to a darker one.

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* The young larva of *Deilephila euphorbiæ* is entirely black on leaving the egg (Schwarz), or pale and becoming black after half an hour (Weismann).

Weismann contends that all those patterns and colors possess only a biological value. The green color, which first appears, corresponds to that of the leaves. But in a large caterpillar one main color would be too apparent; therefore longitudinal lines separate the main color into several fields and diminish the danger, the more so when the caterpillar lives among grasses. The oblique lines afford a similar protection, and are even more effectual when the lines have colored borders, which make them resemble the ribs of leaves. The eye-spots of Chærocampa are said to frighten enemies, and the variegated colors of Deilephila to designate them as not eatable. The dark color of full-grown caterpillars of Chærocampa is said to be owing to the impossibility of being protected by any color, on account of its large size. These caterpillars acquire, therefore, the habit of feeding at night, and hide themselves during daytime under dead leaves. As, therefore, every one of the quoted characters is of biological value, they can be explained by means of natural selection, and the necessity to admit a phyletic, or inborn power (immediate, designing, or ordaining power, Crooke) does not exist. The possibility of the existence of such a power is rejected by Weismann.

The conclusions and statements of Weismann are based upon a number of European species. But it seems that the study of exotic species will show that some of these conclusions cannot stand, or will lose at least a large part of their value. The colorlessness of the newly hatched caterpillars is perhaps not without exception in some tropical species. The succeeding green color belongs to the hypodermal colors, but all the longitudinal and oblique lines and the spots belong to the dermal colors. The dorsal line is the consequence of the situation of the dorsal vessel; probably the subdorsal line and the oblique lines are muscular lines, and the stigma line a consequence of the large longitudinal tracheæ.

The large eye-spots on the thoracical segments indicate the place under which the wings are beginning to be formed. Similar spots, but less strongly developed, are to be found in a number of larvæ of Myrmelionidæ. The formation of the wings necessitates a largely accelerated circulation in those places, and therefore an oxidation of the cuticula. These eye-spots belong to the dermal colors. The very remarkable eye-spot in *Pterogon* (*Thyreus*) *Abbottii* appears in the third stage exactly on the same place where before the tailed appendage existed. The change in this species is very interesting. The second stage has as main color a very light grayish pink, and possesses an orange tubercle, surrounded with black, where the first stage had a tailed appendage. The third stage is either similar to *Pterogon œnotheræ,* dark gray with numerous irregular and very fine paler lines and some darker longitudinal ones, or is black, with large transversal bright yellow bands (indeed so large that the color can also be described as yellow with transversal and longitudinal black bands), and both have instead of a tailed appendage a prominently black and large eye-spot. The differently colored caterpillars represent not the two sexes, as I have raised males which are entirely alike in color and pattern, from both forms of the caterpillar. Both forms live on the same vine (*Ampelopsis quinquefolia*), but the yellow ones are rare. All stages live and feed during the daytime on the vine, the very visible pink ones and the yellow ones, which would need some protection, and the gray ones, which do not need it. I remark purposely that the latter does not go in the daytime on dry stems, as Weismann (p. 80) records for *Pterogon œnotheræ,* but feeds on the green leaves together with the other ones.

The question why this pattern, when considered to be the consequence of the before-quoted causes, is not developed in every caterpillar, is still to be answered. A large number of conclusions of a similar character accepted now-a-days are based on exceptions, if we consider the large number of species which do not agree with them. So feed in North America the very large caterpillars of Chærocampa openly, during daytime, contrary to Weismann's statement for the European species. Exactly in the same manner feed openly in daytime a number of uniform light green caterpillars, which must nevertheless be well protected, as they belong to common species. That the variegated colored ones are repugnant to a higher degree than the not variegated ones, is still to be proved. Both are rarely taken here by birds, as far as I know. That such caterpillars live upon poisonous plants is true for some European species (Slater, Trans. Entom. Soc. London, 1877, p. 205). I believe Weismann's statements are only to be admitted as true ones as far as they go, but not in a general way.

I may state that at least one case is known to me where a difference in feeding caterpillars exaggerated the pattern. An entomologist in Prussia a few years ago divided a large lot of Sphinx caterpillars of the same species, and fed both with the same leaves. The stalks of one lot had been placed in fresh water, and of the other lot in salt water. Both grew very well, but the latter differed considerably in color. Nevertheless the imagos were all alike. The caterpillar of *Hemileuca Maia* feeds in Michigan, New York, and Massachusetts on shrub oak (*Q. ilicifolia*), in Maine and in Nevada (?) on *Spiræa salicifolia.* The caterpillars are very little different, but the imago differs considerably. The first ones are largely black, with more or less narrow white bands; the last ones are largely white only with blackish borders, and sometimes the hairs on both sides of the front part of the thorax are also snow white.

Rev. H. H. Higgins (Quart. Journ. of Science, 1868, vol. v. pp. 323–329, pl. 1) gives some remarks on the proximate origin (the appliances immediately engaged in producing the color pattern) and general configuration of the patches, bands, and spots of color on the wings of Rhopalocera. "In the chrysalis state the patterns of the closely folded wings, the like spots on the right and left wings do not coincide; that which becomes a beautifully formed band, begins as a mere line or a shapeless spot. The simplest type of color presents itself in the plain uniform tint when the scales are all colored alike, which is comparatively rare. At first the scales growing on the membrane upon or near the veins show a freer development of pigmentary matter, and in this manner would arise a kind of primary or fundamental pattern, namely, a pale ground with darker linear markings, following the course of the veins (*Pieris cratægi*). This pattern occurs in most of the families. Let it be supposed that at a given distance from the base a portion of the dark scales begins to diverge on each side from the veins. The dark lines thus formed will meet in the middle of the areas between the veins producing a band of scallops having their concavity towards the base of the wing. A similar band nearer to the base would have its convexities in the same direction. If the latter mode of divergence be quickly followed by the former, a row of annular markings between the veins is the result, the simplest form of annular or ocellate spots. In the pupa state the scheme of the future pattern is fully organized, so that by the extension of the soft wings the pattern of the imago is easily performed. From the vein scales arise all the darker markings, enclosing sometimes the areas of pale, ground tint. The modifications of those areas are performed by a blush, the deepening or the intensifying of the color in certain parts of the wing (*G. Cleopatra*). Besides this comes the gloss by iridescence."

Charles Darwin (Descent of Man, vol. ii. pp. 126–127, fig. 52) speaks of the formation and variability of the ocelli on the wings of many Lepidoptera: "Although we do not know the steps by which these wonderfully beautiful and complex ornaments have been developed the process, at least with insects, has probably been a simple one; for, as Mr. Trimen writes to me, no characters of mere marking or coloration are so unstable in the Lepidoptera as the ocelli, both in number and size."

As far as I know there is nothing more published on this subject. In some few instances I have been able to observe how the pattern is produced. In dragon-flies (Odonata) the thorax is transparent and entirely colorless at the moment of transformation. At this time the muscles are in process of formation. The thoracic muscles of the Odonata are, as is well known, very powerful, and rather exceptional in the shape of their tendons. I observed very strong currents of the blood just along the place where the muscles were developing. The rush of the blood was very much accelerated. Now just outside of these we find in Odonata dark lines or bands, which appear to be the result of the formation of the muscles. *Ubi irritatio, ibi affluxus;* therefore it is not improper to conclude that a powerful action in the development of the muscles is here the cause of a stronger combustion and of an oxidation in the adjacent parts of the external crust of insects. But not the pattern of the thorax alone follows the lines of the muscles. On the head we find a certain pattern corresponding to the muscles of the mandibular apparatus; another one on the segments of the abdomen corresponding to the so-called respiratory or abdominal muscles, and another one on the legs corresponding to their muscles. It is important to remember that those patterns are better and more definitely developed in the most powerful flying Odonata, as in the Æschnina, and especially in the Gomphina. The main color of the Gomphina is yellow of different shades, mostly greenish-yellow, and the stronger the species the larger is mostly the pattern of blackish bands.

I have observed the same proceedings in Cicada just emerging from the nympha skin. On the head, thorax, abdomen, and legs appear similar patterns, corresponding to the muscles or to their insertion places. In fact where a stronger circulation exists in insects, the parts become more strongly chitinized and darker colored.

Should my explanation of these facts be accepted, we shall have taken a step forward in understanding the origin of the pattern. I know very well that among the Odonata patterns exist which do not agree with my explanation, and in one case are even opposed to it.

But though most of the patterns can be explained in this manner, there may exist other factors still unknown explaining the opposite patterns. The explanation given can be considered as admissible as long as the number opposite to it is a comparatively small one.

The pattern on the wings and elytra cannot, of course, be the product of action near or along the muscles, as these limbs are unprovided with them internally. But it seems probable that there the sudden rush of blood and air by the accelerated circulation and respiration during the act of transformation produces the same effect. At least some patterns, the origin of which would be inexplicable, could be understood by it.

If a stream or jet of blood passing through the narrow base of the wingbag should meet within its centre a small obstacle, the previously straight stream would take the form of a funnel. Should this obstacle be a kind of ring, the funnel shape would be retained by the stream, but its central portion would pass undivided through the ring, and upon meeting another obstacle would produce a second funnel. Therefore there may be two or more funnels, one within the other, and a section of them will be circular or elliptical according to the angle at which they reach the inner surface of the wing. A curious fact seems favorably to support my suggestion. Nearly every larger ring or eye-spot of the wings shows a white interruption or spot in some place. Now as it is impossible that any obstacle, such as mentioned before, can be entirely free and isolated in the stream, we must presume that it is somewhere connected with the interior of the body, and is perhaps produced by some prominent ridge or corner, and then the funnel or the ring must be interrupted in some place by this connection. If it is so, this place will not be oxidated (colorless), and will correspond to the white spot mentioned before.

Such patterns of the elytra and wings have to be performed at the time when the wing is still an open bag, and before the transformation. There is still another circumstance which explains some patterns. The walls of the bag which will be later a wing or elytron, are very suddenly enlarged and strongly dilated during the act of transformation. Therefore small rudimentary patterns in the bag will be altered and enlarged by the same proceedings. I know that many patterns of Lepidopterous wings can be easily explained in this way. All the wavy lines and similar marks belong to these patterns. As the ribs or veins of the wings seem to grow faster in transformation than the membrane between them, the wavy shape of the lines would thus be explained. In fact the larger part of the patterns seem to be produced by expansion or by distraction of the pattern, performed in the bag at a period before transformation. It should have been stated before, that the formation of patterns on the wings of Lepidoptera must take place at the time when the scales are still little open bags.

At first my suggestion about the formation of the pattern in such a manner may seem to be strange, and perhaps not admissible. But in thinking over the subject again and again, I have found more and more support for its adoption. I had been puzzled chiefly about the existence of obstacles in the streams of blood. The excellent paper of C. Semper (Zeitschrift f. wissensch. Zool. vol. viii. pl. xv. f. 1) contains a statement of the formation of a layer to close the wing-bags at the base. This layer is formed by a number of cells united gradually by some projections, and the whole may be compared to a kind of cobweb with larger spots at certain intervals. I believe that the presence of such a layer would explain very well the presence of obstacles in the manner before stated.

A striking proof of the appearance of dark color and dark lines along an accelerated circulation is given by the dark coloration around the nipple and along the linea alba in pregnant women. This dark color is not formed by pigment cells, but by the common cells of the mucosa. Around the nuclei of these cells is found deposited fine and homogeneous pigment.

The colors of the pattern are dermal colors. They may, and in fact do, often cover the whole insect. Leydig stated long ago that the eye-spots of the caterpillars of Papilio are dermal colors. All colors, the pattern excepted, are hypodermal colors. The dermal colors are formed during the transformation, before the integument becomes rigid and before the cuticula has finished to enclose safely the colors. The hypodermal colors are formed either after this period or as a main color in previous stages just after hatching, before any pattern exists.

I think this is the proper place to mention the interesting fact called mimicry. In treating of mimicry there have been used indiscriminately very different factors. I have before endeavored to give some preliminary ideas about it, which are perhaps useful in explaining this curious fact. Of course I speak here only of mimicry in colors, of colors imitating the surroundings, as, for instance, the excrements of birds, dry leaves, berries, parts of trees, branches, bark, and whatever is found of them. The mimicry of the form and shape of other insects is even more wonderful, but still unexplained, except as a protection. I have to confess, that just the unexplained mimicry of form seems in some way opposed to my explanation of the mimicry of colors. Science is in such questions still in its infancy, and the first step is always the hardest. Every plausible suggestion is not objectionable till a more convenient one has been given.

As stated before, the dermal colors never change, the hypodermal colors can change. Therefore mimicry of pattern is here excluded, the hypodermal colors being the only ones on which the animal has any influence, either involuntarily by the constant action of the nutritive fluid, or voluntarily.

If it could be proved by facts that by a kind of photographic process the colors of the surrounding objects can be transmitted, a great step towards an understanding of mimicry in color would be attained. The fact is probable, at least in some instances. I know no other explanation, and the discovery that the seeing-purple in the eyes of men and animals retains for a certain time after death the impression of things and faces last seen, is in favor of my hypothesis. The eyes of the insects contain a layer homologous to the seeing-purple, and this layer is a decidedly hypodermal one.

There is not much known about the color of the eyes of insects. It may be said that perhaps all colors have been observed, from black to white, brown, red, blue, green, golden, and in all different shades. The color belongs to the chorioidea, and the pigment is included in cells. Eyes without color pigment do not serve for vision. As the colors are not persistent after death, they belong to the hypodermal ones. Among Arthropods is to be found, just as in Vertebrates, the peculiar organ called tapetum, a luminous colored spot on the underside of the chorioidea. The tapetum is recorded for Arachnidæ, Lepidoptera, and Diptera, and can cover the whole eye or parts of it, or can form certain figures, as in Tabanidæ and other Diptera.

Leydig describes the tapetum of fishes as formed by small plates or lamellæ in very near juxtaposition. Only by a stronger pression the iridescent lamellæ will become separated. Arthropods, for instance Chrysopa, shows in the golden eyes small colored nuclei ; but in other insects (Mantis) these nuclei alternate with iridescent plates. The large Sphingidæ and Noctuidæ possess a peculiar tapetum. A vertical cut through the eye shows underneath the dark pigment a silver-white layer with a reddish front border formed by numerous and very fine tracheæ. The reddish color belongs to the bacillar-layer of the optical nerve.

The Nature of Color and its Formation.

What is color? Where does it come from, and what part of the body is used to produce it? What kind of chemical process brings it out?

The importance of these questions is obvious, but science has not answered them till to-day. Even the questions themselves have scarcely been mentioned. It is a curious fact, though frequently observed, that the nature of the most interesting phenomena is not questioned at all, only because everybody meets them every day and everywhere.

The chemical nature of all colors — optical ones excepted — is undoubtedly proved by the fact that colors can be destroyed partially or entirely by chemical action. The greatest enemy of color is light. The strong and continuous influence of light, principally of sunlight, gradually fades every color, which is not sustained or renewed by the life of the insect. This fact is the more important, as on the other hand the influence of light during life is a color-producing one. But to produce color life is needed, for a continuous fresh supply of matter to be changed into color. As soon as life ceases and fresh matter is no longer supplied, the chemical influence of light becomes too strong, and causes discoloration.

I may here notice that Professor Sachs (Botan. Zeitung, 1863, 1865, and with Askenasy, 1867), by the examination of the influence of light in producing the blossom-colors, arrived at this result, that the development of these colors is not dependent on the influence of light. The size of the blossom and the intensity of its colors are said to depend on fertilization by insects (Wallace).* Therefore on high mountains or in northern regions, where the insect fauna is a small one, the plants have large and intensely-colored flowers, which are easily recognized at great distances. Dr. H. Müller (Kosmos, August, 1880) is of the same opinion, "that the colors of flowers are developed through the fertilization by insects, as he believes, in a progressive manner. Red, violet, and blue are always developed later, by natural selection, than white and yellow. But there is no reason to adopt the theory that the development of the different flower colors always originated from the same primal color, and surely the series of the developed colors was not always identical."

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* Ch. Darwin: The Effects of Cross- and Self-fertilization in the Vegetable Kingdom, 1877.

I am not prepared by my studies to object altogether to the statements of such prominent authorities. But it is well known that plants and animals excluded from light are more or less colorless. Secondly, the number of plants with highly colored flowers which are not fertilized by insects will exceed, perhaps largely, those fertilized by insects. The horticulturists produce year after year in greenhouses new varieties, with larger and more brilliantly colored flowers, but certainly not through fertilization by insects.

During the summer of 1881, chrysanthemums were prepared for a flower exhibition in Boston by a thoroughly experienced and scientific horticulturist. He had kept purposely plants, cuttings from one and the same plant, partly in sunlight, partly not in the dark, but without sunlight. The effect was so striking, that later the judges would not accept as a fact that both kinds came from the same stock. The plants kept in sunlight showed the most brilliant colors, the other were pale and very little colored.

I am not able to understand how this fact could be brought about without acknowledging the influence of light. I quote only this case, though every horticulturist may be able to give similar ones, because the experiment was made purposely, and is doubtless reliable. I think science will need a plausible explanation of such experiments, proving that sunlight was not the acting factor, before the statements of even such a prominent authority as Professor Sachs can be accepted.

The bleaching of the colors of insects by chloride of lime or by certain solutions of it is proved by Dimmok's experiments (Psyche, No. 17, 1875), and by my own recorded before. Perhaps chemical investigation made in a more varied manner, and the use of less strong chemicals, will some day throw more light upon the nature of colors. An interesting observation may here be noticed (J. W. Wilson: Chemical Change of Coloration in Butterflies; Psyche, No. 75, 1880). In coloring a proof plate of *Limenitis arthemis* for the well-known book by Mr. W. H. Edwards, the insect was inclosed in a shallow glass box, and Miss Peart, the artist, had fastened a bit of cotton inside with a little undiluted carbolic acid. When the plate was sent to Mr. Edwards, rich purple had been painted where the insect is metallic blue or green. The colors of the type had been changed by the acid. Several weeks later the purple disappeared, and the insect showed again its proper colors. Carbolic acid, being a comparatively weak acid, is more easily neutralized; moreover, being volatile, its effects are more transient than those of stronger acids, which change the colors. After such a change alkali only partially restores the proper colors.

The use of benzine affects mostly yellow and orange wings of Lepidoptera, changing these colors into isabell. The application of tobacco-smoke changes pink flowers of roses into light-green ones, and its effect on butterflies is visible, but less marked. Light-brown insects preserved in dilute carbolic acid become much darker, nearly blackish, and they retain this color after having been taken out of the acid.

By the chemical analysis of chitin a certain part was found apparently representing the coloring matter. It was insoluble in water, alcohol, and ether, amorphous, and probably resinous. This matter can be precipitated by acids from a solution of potash.

I was not able to find in the literature sufficient information about the chemical origin and nature of colors. Perhaps some recent publications may throw light upon the subject. Mr. M. Nencki (Bericht. deutsch. chem. Gesell. 1874, vol. vii. p. 1593) stated that indol — the coloring radical of indigo — can be produced through digestion of albumen by pancreas juice. The fact was denied by Mr. Kühne (ibid. 1875, vol. viii. p. 206), in so far as the production of indol was affirmed, but he believed it was produced by the fermentation of the juice, or by the numerous bacteriæ commonly found in the pancreas. Mr. M. Nencki reported later (ibid. 1875, vol. viii. p. 336) that he had succeeded in the production of indol from albumen only. The reddish oil — indol-coloring substance — gives with sufficient nitric acid a red color, with less a violet color (ibid. p. 722). Out of the albumen was produced 0.5 per cent nitric acid, nitrosoindol. By boiling the red coloring substance a brown one is produced, which gives in alcoholic solution of kali or natron a green color, with sulphuric acid a purple one.

In 1868 Messrs. Gräbe and Liebermann had shown that madder-lake can be obtained out of anthracen, a kind of coal-camphor. The consequence of this discovery was, that everywhere the culture of madder was given up entirely. Since that time Professor Bayer in Munich has endeavoured to produce an artificial indigo (Nature, vol. viii. p. 251; vol. xxiii. p. 390; vol. xxv. p. 593; Kosmos, 1881, vol. v. p. 61). He proved the possibility of producing it from protein bodies; but the artificial indigo would be much more expensive than the natural one. In 1878 he obtained small indications of indigo out of phenyl-acetic acid, a product of coal-tar. In 1880 he got indigo out of cinnamic acid, which is made out of toluol, also contained in the coal-tar. The cinnamic acid was changed by nitric acid into a nitrum combination, and afterwards changed by brom into dibromid. This latter in contact with alkali produces indigo. But this indigo also is more expensive than the natural one. I am not able to find more concerning the production of color in chemical literature.

All fats contained in animals and plants are glycerids of fat acids. A large series of fat acids consists always of two atoms of oxygen combined with a number of atoms of carbon, and always twice as many atoms of hydrogen. Of these acids the simplest is formic acid, (CH_2O_2), which, is common in insects, and also to be found in some plants (Urtica).

These acids are extensively developed in some insects living together in numerous societies, as in ants and white ants, but, as far as I know, not in bees or wasps. The acid is sometimes much condensed, and if one strikes a hill with the hand, it will smell strongly of acid. If in winter time, when hills are closed outside, and of course the acid in the hill is more concentrated, one tries to work with the fingers into the hill, to collect Myrmecophiles, the tips of the fingers are sometimes affected as if they had been put in very strong acids. The same is stated of tropical species of white ants living in very strongly built hills. The acid is also reported as corrosive for metals.

Uric acid is largely represented in Arthropods, and only doubtful for Arachnids and Crustacea. To the rich literature about the presence of uric acid in insects, Krukenberg,* p. 28, adds, after his own observations, twenty-eight species. It is not present in *Apis mellifica*, nor in the excrements and in the rectal glands of *Tetrix bipunctata*, of *Locusta viridissima*, and some other Orthoptera; also not in some caterpillars and in the larvæ of *Cimbex variabilis*. He never found a species which contained uric acid in the fat body, and none in the intestinal canal and in the Malpighian vessels. The insects contain, besides glycogen, leucin, tyrosin, hæmoglobin, and peptic-tryptic and diastatic enzyms.

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* C. Fr. W. Krukenberg: Vergl. physiolog. Studien an den Küsten d. Adria, 1880, 1881, vol. iii. p. 62.

Perhaps there exists some stronger acid in some insects. One observation made by myself can scarcely be explained in any other way. A large species of Mygale, having been many years in alcohol, was taken out of it and exposed on a glass slide near the stove to a moderate heat. When it was dried, I was astonished to find the whole slide injured by a corrosive acid. Examined with the microscope, the surface of the slide was covered all over with fine short and mostly parallel lines, rough as if cut out with a diamond. As there is no acid known which injures glass, fluor acid excepted, the fact cannot be explained; but I am quite sure that I was not mistaken in my observation.

I am not able to give any further statements on fat, fat acids, and other acids, because nothing more is known about them. My conclusions are as follows: —

It is certain that a color (indigo) is produced as result of the digestion of albumen.

It is certain that fat is produced by digestion out of albumen.

It is certain that colors of insects are combined with fat. Therefore it seems probable that the colors of insects are chemically produced by a combination of fats or fat acids with other acids or akalis by the influence of air, light, and heat.

It should not be overlooked that anilin is the product of a distillation of the oily parts of coal or peat. Colorless anilin has no alkaline reaction, but neutralizes acids. Everybody knows the variegated and beautiful colors originating from anilin combinations, and it is not a daring conclusion to presume that colors of animals and plants have a related origin and nature. I am assured by Professor W. Hempel, Dresden, Saxony, that in the Gulf of Naples a mollusk has been found which contains aniline colors.

The very obvious question, "Does the food have any influence on the colors of insects?" is answered as often in the affirmative as in the negative.* I have stated before that Sphingid caterpillars fed on plants placed in salt water showed colors different from the caterpillars fed with the same plant placed in fresh water. But the imago showed no difference whatever. On the other hand, the imago of the American *Hemileuca maja* shows the typical black form whenever the caterpillar feeds on *Quercus ilicifolia*, as in Massachusetts, New

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* R. MacLachlan, Entom. Weekly Intelligencer, London, 1861, No. 254: "Variation caused by the Food of the Larva does not exist."

York, and Michigan. But the pale variety, *H. Nevadensis*, occurs where the caterpillar feeds on *Spiræa salicifolia* in Maine, and probably farther in the west. The Caterpillars are slightly different in color. *Actias luna*, fed in Europe on the European walnut, is slightly different in color of the wings from those fed in America on the American walnut. The specimens from Texas are more brilliantly colored than those from New England. I have seen in the Museum in Berlin, Prussia, a large box filled with different varieties of the imago of *Bombyx caja*, and was told by Professor Klug that a number of them were artificially produced by feeding the omnivorous caterpillar with different kinds of food. The most abnormal variety came from caterpillars fed with crumbs of dry bread. Perhaps similarly reliable facts might be found in the literature. Mr. Speyer has given, as related before, some information concerning a different shade of the colors of moths which are found in America as well as in Europe. But there are probably different factors working together to produce these variations.

Krukenberg,* in his elaborate paper, "Ueber thierische Farbstoffe und deren physiologische Bedeutung," comes to the conclusion that the change of color (in perfectly developed insects) is a consequence of the change of food, and can be explained by the alteration and mutation of the pigments through heat and light. His experiments were made for the purpose of finding the cause of the turning into yellow or red by green grasshoppers in autumn. He tries to answer two questions: First, does the pigment of grasshoppers originate directly out of the food, and does it consist of pure chlorophyll or a substance containing chlorophyll, or is it to be accepted as a peculiar production of the organism? Second, is the color the consequence of only one pigment, or of several? His detailed answer is as follows:

"It is evident that the green color of the grasshoppers is the consequence of several different pigments, which can be separated by chemical process."

The immersion of the green grasshopper in ether colors it yellow, and the grasshopper becomes cochineal red. The same is observed when insects are treated with hot water or alcohol. The turning to cochineal red is not the consequence of a chemical mutation of the yellow-green pigment, but solely of its extraction, and the subsequent appearance of the red color, which was formerly covered. If the grasshopper or its wings are subjected to stronger heat, both pigments disappear at the same time. Krukenberg believes it to be very probable, after his experiments, that the light has a prominent influence on the color of insects, and that the light turns to red the insects which were green during the summer. Spectral analysis makes it evident that the green color has no connection with chlorophyll.

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* C. Fr. W. Krukenberg: Vergl. physiolog. Studien an den Küsten d. Adria, 1880, 1881, vol. iii. p. 62.

It is often denied by entomologists that food has any marked influence on color, as it is observed that in many cases caterpillars of the same species feeding on the same plant show very different colors, as, for instance, many Sphingidæ, cankerworm, and others.

Perhaps *Coccus cacti* derives its coloring matter from the cactus; but I was puzzled to find that some grubs of a beetle from Peru, preserved in alcohol, had colored the alcohol rather intensely with cochineal color. I do not know whether they live on the cactus, but it can hardly be presumed. That other insects prepare a coloring matter is well known from the May-beetles in Europe. An umber-brown color, good for use, was prepared from them by distillation, and used at the end of the last century. Mr. G. B. Buckton * and Mr. Sorby † have published very interesting notes and experiments upon the coloring matter of the Aphides. The somewhat condensed conclusions are: —

1. The purple coloring matter appears to be a quasi-living principle, and not a product of a subsequent chemical oxidizing process. Mounted in balsam or other preserving fluids, the darker species stain the fluid of a fine violet.

2. As autumn approaches and cold weather reduces the activity of the Aphides, the lively greens and yellows commonly become converted into ferrugineous red, and even dark brown, which last hue in reality partakes more or less of intense violet or purple. These changes have some analogy with the brilliant hues assumed by maple and other leaves during the process of slow decay.

3. Aqueous solution of crushed dark-brown and yellow-green varieties of Aphides originate different colors with acids and alkalies. The chief difference consists in an alkali changing the solution of green Aphides into a gamboge-yellow, instead of a purple, as in the brown Aphides.

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* G. B. Buckton: Monograph of the British Aphides, vol. ii. p. 167. London, 1879.

† Sorby: On the Coloring Matter of some Aphides. Quart. Journ. Microsc. Soc. vol. ix. p. 352. London.

4. In the generality of cases coloring matters, such as indigo, Indian yellow, madder-lake, and the like, do not separately exist in the substance of vegetables, but the pigments are disengaged through fermentation or oxygenation. Again, alizarin itself is reddish yellow, but alkaline solutions strike it a rich violet, just as we find them act towards the substance which Mr. Sorby calls Aphidilutein.

5. Mr. Sorby's four stages of the changes effected by the oxidation of Aphideine produce four different substances.

The different colors produced by the use of different chemicals must be compared in Mr. Buckton's paper. But there can be no doubt that here colors are produced chemically out of protein-bodies, — a fact somewhat homologous to the before-quoted artificial production of indigo.

The influence of temperature on the colors of the imago of Lepidoptera was first shown by Mr. Dorfmeister. He proved that a higher temperature changes the reddish-yellow of the hind-wings of *Bombyx caja* to minium, a lower temperature to ochreous yellow. The changing of spring-races of butterflies into autumn-races by putting the chrysalis on ice, the well-known experiments made by Mr. W. H. Edwards and Prof. Weismann and others, show unquestionably the influence of temperature on colors. Probably here the change is the effect of a surplus of nitrogen. The water absorbs a small quantity of air, but in such a manner that this air contains less than two parts (1.87) of nitrogen to one part of oxygen, instead of four parts of nitrogen. Therefore an excess of nitrogen in the surrounding air must be the consequence, as is the case in the iced chambers of fruit-houses, where the oxygen is purposely rarefied in relative quantity. By this nitrogen, together with the nitrogen contained in the chrysalis, life and development are retarded to a minimum; but the chemical action which produces colors will work nevertheless to a certain extent. Therefore a change in the colors of the imago is the necessary consequence, and this change affects probably the pattern, which is, as stated before, produced largely by oxygen, which is here rarefied.

Goethe has characterized the yellow and related colors as acid ones, the blue and related as alkaline colors. He states that vegetable yellow colors can be changed by alkali into red, or even into blue red.

For plants the predominant color is green, for insects brown; both of which are called indifferent colors.

Final Conclusions.

If color and pattern are produced in a purely mechanical manner, as Prof. Weismann contends, it ought to be possible to explain and to prove this mechanical manner, if we will go beyond the simple belief that it is so.

The foregoing review contains all that is known about these questions: —

1. That some colors of insects can be changed or obliterated by acids.
2. That two natural colors, madder-lake and indigo, can be produced artificially by the influence of acid on fat bodies.
3. As protein bodies in insects are changed into fat bodies, and may be changed by acids contained in insects into fat acids, the formation of colors in the same manner seems probable.*
4. That colors can be changed by different temperature.
5. That the pattern is originated probably by a combination of oxygen with the integuments.
6. That mimicry of the hypodermal colors may be effected by a kind of photographic process.

In comparing these still insufficient data with the statement — that color and pattern are produced in a purely mechanical manner, and are the consequences of natural selection, of adaptation, and of inheritance, — we must, if we wish to go beyond belief, directly exclude inheritance, as after the statement of Professor Weismann himself† it is entirely unknown how inheritance works; even the question itself is still entirely untouched. We must further exclude natural selection and adaptation, as both are (according to Professor C. Semper ‡) only able to begin to work after pigment is produced and after a change of the pattern has begun.

What is then left to justify our accepting a purely mechanical manner but the simple belief that it is so?

I am convinced that color and pattern are produced by physiological processes in the interior of the bodies of insects.

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* Dr. R. Sachse: Die Chemie und Physik der Farbestoffe, Kohlenhydrate u. Proteinsubstanzen, p. 288 sqq. Leipzig, 1877.

† Dr. A. Weismann: Die Dauer des Lebens, 1882; and Studien, vol. ii. p. 296.

‡ Professor C. Semper: Die natürlichen Existenz-bedingungen der Thiere, 1880. Vol. i., p. 265; vol. ii. p. 232.